Varieties of attention and of consciousness: evidence from neuropsychology

Paolo Bartolomeo[1-3]

1. INSERM UMR_S 610, IFR 70, Hôpital Salpêtrière, Paris, France
2. UPMC Univ Paris 06
3. Fédération de Neurologie, AP-HP, Hôpital Salpêtrière, Paris, France

Address correspondence to:

Paolo Bartolomeo

INSERM UMR_S 610
Pavillon Claude Bernard
Hôpital Salpêtrière
47 bd de l'Hôpital
F-75013 Paris - France
phone +33 (0)1 42 16 00 25 or 58
FAX +33 (0) 1 42 16 41 95
Email: paolo.bartolomeo@chups.jussieu.fr
Web: http://marsicanus.free.fr/

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Abstract. Do we need to attend to an object in order to be conscious of it, and are the objects of our attention necessarily part of our conscious experience? A tight link between attention and consciousness has often been assumed, but it has recently been questioned, on the basis of psychophysical evidence suggesting a double dissociation between top-down attention and consciousness. The present review proposes to consider these issues in the light of time-honored distinctions between exogenous and endogenous forms of attention and between primary and reflective forms of consciousness. These distinctions shed light on results from several sources of evidence, including patterns of performance of brain-damaged patients with visual neglect. These findings strongly suggest that exogenous attention is a necessary condition for primary visual consciousness to emerge. Visual neglect, which typically results from damage to fronto-parietal networks in the right hemisphere, entails an inability to orient to and to detect contralesional objects. Importantly, neglect patients are not only unable to verbally report contralesional objects, but may also act as if these objects did not exist, for example by bumping into them, thus suggesting an impairment of primary perceptual consciousness. Less frequently, neglect patients may instead show forms of "implicit" knowledge of neglected items, perhaps indicating a deficit of more reflective forms of consciousness, such as those subserving verbal reportability. The integration of several sources of evidence, such as phenomenology, experimental psychology and neuroscience, is needed to further explore the taxonomy of these processes and to identify their neural correlates.

1. Introduction

Cognitive neuroscientists have often considered attentional processes as “the mechanisms of consciousness” (Posner, 1994). Introspection does suggest that we need to attend to an object in order to be conscious of it, and that the objects of our attention are necessarily part of our conscious experience. A tight link between attention and consciousness was also postulated by William James, who vividly wrote in a often-cited passage: "Millions of items of the outward order are present to my senses which never properly enter into my experience. Why? Because they have no *interest* for me. *My experience is what I agree to attend to.* Only those items which I *notice* shape my mind - without selective interest, experience is an utter chaos" (James, 1890, p. 402).

More recently, however, the relationship between attention and consciousness has become a matter of debate. In particular, the commonly accepted notion that attention is necessary and sufficient for consciousness has been challenged. For example, Koch and Tsuchiya (2007) reviewed psychophysical evidence on normal participants and concluded that "top-down attention and consciousness are distinct phenomena that need not occur together".

It is clear that attention and consciousness describe different processes, which to some extent belong to distinct conceptual categories. Attention has observable behavioral correlates in terms of response times/accuracy and perceptual discrimination (Pashler, 1998). Consciousness, on the other hand, refers to subjective experience, not necessarily reflected in verbal reportability (Dalla Barba, 2002). Despite this conceptual distinction, however, evidence from both normal participants and brain-damaged patients seems to confirm the introspective intuition

of a tight relationship between attention and consciousness. In particular, evidence suggests that some attentional processes can be a crucial antecedent to consciousness, along the lines proposed by William James.

But in order to be able to appreciate such relationships, it is important to consider two time-honored distinctions concerning (1) attention and (2) consciousness.

2. Attention: exogenous vs. endogenous

Biological organisms live in an environment cluttered with a multitude of objects. To behave in a coherent way, organisms need to select objects appropriate to their goals, and to quickly react to unexpected, dangerous predators. On the other hand, because of capacity limitations, they must be capable of ignoring other, less important objects. Thus, objects in the world compete for recruiting the organism's attention, i.e. to be the focus of the organism's subsequent behavior. Neural attentional processes resolve the competition (Desimone & Duncan, 1995), on the basis of the organisms' goals and of the sensory properties of the objects, by giving priority to some objects over others. In ecological settings, animals usually orient towards important stimuli by turning their gaze, head and trunk towards them (Sokolov, 1963). Orienting movements align the stimulus with the part of the sensory surface with highest resolution (e.g., the retinal fovea). This allows further perceptual processing of the detected stimulus, for example its classification as a useful or as a dangerous object. Orienting movements are thus a typical form of "embodied" cognition (Ballard *et al.*, 1997), that is a process in which body movements are necessary to the processing of information. Thus, orienting movements optimize the processing resources, with a segregation of mechanisms dedicated to simple detection from resources performing more

complex identification tasks, based on object shape, color, etc. (Di Ferdinando *et al.*, 2007). In Posner's terms, *orienting*, consisting in the alignment of attentional processes to an object in space, precedes *detecting*, which refers to the subject's becoming aware of the object (Posner *et al.*, 1980).

Visuospatial attention can be directed to an object either exogenously, or in a bottom-up way, such as in visual pop out driven by perceptual saliency, or endogenously, in a top-down fashion, determined by the subject's goals. As discussed above, this distinction makes ecological sense, because in everyday life we must be able to maintain our goals, e.g. crossing the street to buy a newspaper, while coping with unforeseen but important events, e.g. avoiding an unexpected danger, such as a car coming at high speed while we cross the street. In other words, we need mechanisms capable of dealing with conflicting needs: sustain our attention against distractors, but also interrupt sustained attention where appropriate (Allport, 1989).

Once again, this distinction was already recognized by William James, who distinguished "passive, reflex, non-voluntary, effortless" attention from "active and voluntary" attention (James, 1890, p. 416). Evidence supporting this distinction comes from a variety of sources, such as experimental psychology, basic and cognitive neuroscience.

2.1. Evidence from experimental psychology

Much of what we know about the operations of visuospatial attention comes from the work of the Posner group (reviewed in Posner, 1980). These authors developed a manual response time (RT) paradigm to study the spatial orienting of attention. In this paradigm, participants are presented with

three boxes horizontally arranged on the computer screen. They fixate the central box and respond by pressing a key to a target (an asterisk) appearing in one of the two adjacent boxes. The target is preceded by a cue designating one of the lateral boxes. The cue can be either 'central' (a centrally presented arrow pointing toward one of the two lateral boxes in which the target is to appear), or 'peripheral' (a brief brightening of one lateral box). *Valid* cues correctly predict the box in which the target will appear, whereas *invalid* cues indicate the wrong box. Valid cues usually improve accuracy and RTs for target detection, whereas invalid cues have a detrimental effect on performance; the advantage for valid cue-target trials and the cost for invalid trials is referred to as cue validity effect. This effect suggests that the cue prompts an attentional orienting toward the cued location, which speeds up the processing of targets appearing in that region and slows down responses to targets appearing in other locations. The degree of predictiveness of cues influences the type of attentional processes. Often, a majority (e.g., 80%) of cues are valid; in this case, most cues correctly predict the future site of the target, and are said to be *predictive*. But cues can also be *non-predictive*; in this case, the target will appear with equal probability in the cued or in the uncued location. Peripheral non-predictive cues attract attention automatically, or exogenously (Jonides, 1981; Müller & Rabbitt, 1989). This exogenous attentional shift (revealed by a cue validity effect) is typically observed only for short stimulus onset asynchronies (SOAs) between cue and target. For SOAs longer than ~300 ms, however, uncued targets are responded to faster than cued targets (Lupiáñez *et al.*, 2006; Posner & Cohen, 1984), as if attention was inhibited from returning to previously explored objects. This phenomenon has been labeled *inhibition of return* (Posner *et al.*, 1985). When peripheral informative cues are used, on the other hand, the cue validity effect persists even at longer SOAs, thus suggesting that the initial exogenous shift is later replaced by a slower, more endogenous shift toward the same location (Müller & Findlay, 1988)(Fig. 1). This endogenous shift would be motivated by strategic

considerations, because subjects are aware that targets will appear with high probability at the cued location (but see section 3.1. below).

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Fig. 1 about here

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2.2. Evidence from neuroscience: the neural bases of spatial attention

Neurophysiological data in the monkey indicate the existence of fronto-parietal (FP) networks related to attentional processing (Chafee & Goldman-Rakic, 2000). These networks function in an integrated manner during orienting. A recent study demonstrated that during visual search of pop out targets, presumably involving exogenous orienting, activity starts in the parietal lobe. On the other hand, during feature conjunction search, which demands more endogenous, top-down processes, activity begins in the frontal lobe (Buschman & Miller, 2007). Importantly, however, in this study sustained FP activity was a neural correlate of both pop-out search and feature conjunction search, suggesting that both exogenous and endogenous forms of attention require coordinated activity in FP networks.

Current neuroscientific evidence in humans also suggests that large-scale networks on the lateral surface of the hemispheres, including portions of the parietal and of the frontal lobes, are important for orienting of attention to objects or locations in space. For example, fMRI experiments reviewed by Corbetta and Shulman (2002) have identified a bilateral FP network implicated in top-down orienting, including the superior parietal lobe and the superior frontal

lobe. A more ventral FP pathway, including the temporo-parietal junction and the inferior frontal lobe, and lateralized to the right hemisphere, is instead active when subjects have to reorient their attention from an expected location to an unexpected one, and might thus be an important condition for exogenous orienting to occur[1]. (Corbetta & Shulman, 2002) (Fig. 2).

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Fig. 2 about here

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Consistent with these notions, several distinct FP systems have been demonstrated in the monkey (Rizzolatti & Matelli, 2003). These systems, arranged in a dorso-ventral fashion, are connected by distinct white matter long-range pathways, including branches of the superior longitudinal fasciculus (SLF) (Schmahmann & Pandya, 2006). Preliminary results suggest a similar organization in the human brain (Thiebaut de Schotten *et al.*, in press) (Fig. 3).

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Fig. 3 about here

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It is tempting to speculate that these FP systems subserve distinct attentional processes. For example, the dorsal attentional network postulated by Corbetta and Shulman (2002) might be

[1] Kincade et al (2005) did not detect increased activity in the right temporo-parietal junction during exogenous orienting per se, i.e. during the time interval between the cue and the target. However, the temporal resolution of fMRI is insufficient to detect events such as exogenous-related facilitation, which typically reaches a maximum around 100ms after cue onset (Müller & Rabbitt, 1989).

connected by the SLF II, whereas the ventral network might be linked by the SLF III (Bartolomeo *et al.*, 2007b). A further, still more ventral system implicated in attentional processing might be connected by the inferior fronto-occipital fasciculus, a pathway running in the depth of the temporal lobe (Catani, 2006; Urbanski *et al.*, 2008). It remains to be seen if and how the exogenous/endogenous distinction precisely maps onto these different FP systems.

2.3. Human neuropsychology: The case of visual neglect

Clinical evidence from brain-damaged patients also supports the distinction between exogenous and endogenous attention. When damage to the right hemisphere disrupts the integrated functioning of the FP attentional networks (Bartolomeo, 2006; Bartolomeo et al., 2007b; He *et al.*, 2007; Thiebaut de Schotten *et al.*, 2005), patients may lose awareness for events occurring in portions of space contralateral to their lesion, a complex of symptoms collectively known as visual neglect (see Bartolomeo, 2007; Husain, 2008, for recent reviews). When exploring a visual scene, patients with left neglect behave as if left-sided objects did not exist. They do not eat from the left part of their dish and bump their wheelchair into obstacles situated on their left. They have a tendency to look to right-sided details as soon as a visual scene unfolds, as if their attention were "magnetically" captured by these details (Gainotti *et al.*, 1991). When copying a linear drawing, they fail to copy the left part of the whole scene or of objects therein (Fig. 4).

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Fig. 4 about here

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These patterns of performance suggest that neglect patients have problems of attentional

orienting towards left-sided items (Bartolomeo & Chokron, 2001). Typically, however, neglect patients' deficits of spatial attention are not generalized, but concern first and foremost exogenous orienting (see Bartolomeo & Chokron, 2002a, for review), with a relative sparing of endogenous orienting (Bartolomeo *et al.*, 2001). For example, the mere presence of visual objects on the non-neglected side can dramatically increase patients' deficits. This has repeatedly been shown on paper-and-pencil tasks (Bartolomeo *et al.*, 2004; Chokron *et al.*, 2004; Mark *et al.*, 1988) and on response time experiments, where responses to left-sided targets are dramatically slowed down by the previous presentation of right-sided visual cues (Bartolomeo et al., 2001; Posner *et al.*, 1984), or even by the mere presence of the placeholder boxes in which the target will appear (D'Erme *et al.*, 1992; Rastelli *et al.*, 2008). Importantly, neglect increases also when right-sided stimuli are irrelevant to the task or useless to predict the target location (Bartolomeo et al., 2001; D'Erme et al., 1992; Friedrich *et al.*, 1998; Rastelli et al., 2008; Siéroff *et al.*, 2007). This particular feature strongly suggests that irrelevant right-sided stimuli increase left neglect by exogenously capturing patients' attention, such as in the "magnetic attraction" phenomenon.

Taken together, this evidence raises the possibility that in neglect there is an asymmetry of processes involved in exogenous orienting, with attentional capture form right-sided events being easier and/or faster than capture form left-sided events. This asymmetry might result from either an excessive facilitation for rightward orienting (Kinsbourne, 1993), or a deficit of leftward orienting (Heilman *et al.*, 1993; Riddoch & Humphreys, 1987), or both (Bartolomeo & Chokron, 1999). Be that as it may, what is of interest here is that an attentional bias primarily affecting exogenous orienting can lead to a dramatic lack of awareness for a substantial part of the patients' visual world. This is reminiscent of situations in which normal individuals show (less dramatic) forms of unawareness for

perceptually salient stimuli, such as in the "change blindness" experiments (O'Regan *et al.*, 1999), whereby people can miss salient visual objects if their attention is oriented elsewhere. These phenomena suggest that processes underlying attentional capture, such as exogenous orienting of attention, are necessary for our primary consciousness of the visual world (Bartolomeo & Chokron, 2002b). The fact that, as a consequence of their attentional bias, neglect patients are not only unable to verbally report contralesional objects, but they may also act as if these objects did not exist at all, for example by bumping into them, suggests an impairment of primary perceptual consciousness in these patients.

In normal individuals, attentional capture can be modulated by top-down processes, such as those related to the subjects' goals and strategies (Folk *et al.*, 1992; see Ruz & Lupiáñez, 2002, for review and discussion). Can neglect patients use these processes to compensate for their neglect and become aware of left-sided objects? Evidence from patients who clinically recover from neglect, either spontaneously or after rehabilitation, suggests that recovered patients actually learn to compensate for an early right attentional capture with a later leftward orienting (Mattingley *et al.*, 1994), which probably takes advantage of endogenous mechanisms (Bartolomeo, 1997, 2000). But also patients with chronic neglect are able to exert some top-down control over their attentional orienting (Bartolomeo et al., 2001; Duncan *et al.*, 1999; Làdavas *et al.*, 1994; Smania *et al.*, 1998). Perhaps they can do so only in narrow experimental sets, and not in real life, because their endogenous orienting processes are too slow to cope with the ever-changing visual environment of everyday life (Bartolomeo et al., 2001). One may thus conclude that (relatively) preserved endogenous processes are insufficient to obtain full awareness of the visual environment, if attentional capture is laterally biased.

Most neglect patients are unaware of their condition, or, in neurological terms, "anosognosic".

However, some of them, perhaps the most intellectually gifted, are able to reach some rational knowledge about their neglect. Unfortunately, this knowledge is insufficient to overcome their deficits in most situations of everyday life. For example, the famous film director Federico Fellini, after having suffered from a right hemisphere stroke, was well aware of having signs of left neglect, and jokingly asked to include his new condition of "neglector" in his calling card, but nevertheless continued produce to funny drawings lacking their left part, or to bisect asymmetrically horizontal lines (Cantagallo & Della Sala, 1998). Thus, in this case a dissociation occurs between forms of consciousness based on intellectual acknowledgment, and available to verbal report, and more primary forms of spatial awareness (or lack thereof) (see section 3 below).

2.4. “Implicit” knowledge in visual neglect and interhemispheric disconnection

But neglect patients may demonstrate other intriguing patterns of dissociation involving consciousness. Although they typically fail to explicitly acknowledge the presence of left-sided objects, these “neglected” objects can nevertheless affect their behavior. For example, patients may fail to produce the appropriate manual response to left-sided stimuli despite having looked at them (Làdavas *et al.*, 1997). Or, they may incorrectly state that a left-sided item was absent, but responding faster than for *really* absent items (Laeng *et al.*, 2002; Mijovic'-Prelec *et al.*, 1994). Patients may also show semantic priming from neglected items (Berti & Rizzolatti, 1992). These puzzling patterns of behavior suggest that some patients have some implicit (or “covert”) knowledge of otherwise neglected items (see, e.g., D'Erme *et al.*, 1993; Volpe *et al.*, 1979). Perhaps in these patient some residual capacity of leftward exogenous orienting can support a limited degree of primary consciousness for neglected items,

insufficient to lead to the more reflective forms of consciousness necessary to accurate verbal reportability. If orienting is impaired, for example because FP networks are dysfunctional such as in neglect, the target may at best evoke regional neural activity (e.g. in the extrastriate visual regions, see Vuilleumier *et al.*, 2001) and implicit cognitive processing, and at worst only local neural activity (e.g. in or around V1) with no detectable behavioral correlate.

Some of the patterns of performance labeled as signs of implicit knowledge in neglect are reminiscent of behaviors shown by patients who underwent a surgical section of their corpus callosum (so-called split-brain patients). In these patients, callosotomy, performed in order to control intractable epilepsy, impairs communication between the hemispheres. Thus, the "speaking" left hemisphere, which has no access to information coming from the left visual field, may produce confabulatory verbal responses to objects presented in this hemifield. In an often cited example (see Gazzaniga & Baynes, 2000), a split-brain patient was shown tachistoscopically the pictures of a snow scene in the left visual field/right hemisphere and of a rooster claw in the right field/left hemisphere. When the patient was presented with multiple pictures and asked to use each hand to choose those matching the bilateral displays, his right hand chose the picture of a rooster, and his left hand, driven by the right hemisphere, appropriately chose a shovel as a match for the snow scene. At debriefing, however, the patient, whose left hemisphere had not seen the snow scene, confabulated that the shovel was needed to clean out the chicken house.

The analogy is impressive with some cases of "implicit" knowledge in neglect. When a neglect patient was shown the drawing of two houses identical in all respect, except that one has flames coming from its left part, she stated that the houses were identical, consistent with her left neglect. However, when asked which house she would have preferred to live in, after having commented about

the "silliness" of the question, she consistently chose the non-burning house (Marshall & Halligan, 1988). Similar to split-brain patients, these neglect patients may offer confabulatory explanations at debriefing, such as that the non-burning house had an extra fireplace (Bisiach & Rusconi, 1990; Doricchi *et al.*, 1997; Manning & Kartsounis, 1993). This analogy may suggest that interhemispheric disconnection may contribute to some neglect signs, which would result from the activity of an isolated left hemisphere (Geschwind, 1965b). Callosal disconnection has indeed been anatomically demonstrated in several cases of left neglect (see Bartolomeo et al., 2007b, for review and further discussion).

More direct evidence on the role of an isolated left hemisphere in visual awareness comes from the study of visual extinction. Patients with left extinction, which is often but not always associated with neglect, can detect left- or right-sided stimuli when presented in isolation. On bilateral stimulation, however, patients only report the right-sided stimulus. Thus, the right-sided stimulus is said to "extinguish" the left one. In a right brain-damaged patient with left extinction, disruption of interhemispheric transfer of visual information was demonstrated by recording of evoked potentials (Smania *et al.*, 1996). When this patient was presented with bilateral visual stimuli, she often reported seeing only the right-sided stimulus. Remarkably, however, bilateral stimuli were detected much more often, when, instead of the verbal response (saying "two"), she had to use motor responses with no preferential triggering by one hemisphere (e.g. moving the eyes upward) or a response requiring bilateral muscular control (e.g. lowering the chin) to report double stimuli. In this case, left-sided stimuli tended to be neglected especially when the response was verbal and thus chiefly controlled by the left hemisphere. Thus, an important requirement for reflective consciousness and accurate verbal reportability for items processed by the right hemisphere could be the integration of this information

with left-hemisphere based resources.

2.5. Visual neglect: Implications for research on consciousness

The case of visual neglect and related disorders such as extinction invites the following conclusions concerning consciousness. (1) Exogenous attention, which is selectively impaired in neglect, may be critical for conscious processing of a visual event. (2) Consciousness can not be reduced to a homogeneous phenomenon defined by verbal reportability, because of the possibility of inconsistencies between verbal and nonverbal forms of report in neglect or split-brain patients. (3) A network-scale integration of activity from distinct brain systems, both at intra- and at inter-hemispheric levels, appears to be a necessary condition for at least some forms of consciousness to emerge.

Conclusion (1) is relevant to the discussion of the examples of "consciousness without top-down attention" given by Koch and Tsuchiya (2007). While it may be true that top-down attention is not necessary for consciousness to emerge (Koch & Tsuchiya, 2007), it would be more difficult to negate that some form of exogenous attention is a necessary condition for consciousness. For example, even if I may move away without much thinking (or endogenous attention) from a car running towards me, it is unlikely that I remain completely unaware that “something” passed near me at high speed, unless I have a neurological condition like visual neglect (in which case I would probably be hit by the car).

Neglect also suggests that "conscious" processing may take place at different levels of integration. Brain damage may give rise to peculiar patterns of performance as a result of the isolation of processes that were previously integrated in large-scale networks, with consequent loss of the

possibility of the emergence of a conscious correlate. This lesion-induced modularity can be the result of damage to long-range white matter pathways. White matter disconnections may act as the "isolating" mechanisms in human neuropsychology in general (Catani & ffytche, 2005; Geschwind, 1965a), and in neglect in particular (Bartolomeo et al., 2007b; Doricchi *et al.*, in press). As a result of this pathological, acquired modularity[2], conflict may arise between processes that are not anymore integrated. Patients' behavior may then reflect the compromise result of a strive for coherence among conflicting processes.

3. Consciousness: primary vs. reflective

These considerations and the possibility of inconsistencies between different forms of conscious report lead to the second proposed distinction, which distinguishes primary and reflective forms of consciousness. In the phenomenological tradition, it has often being observed that there are forms of consciousness that do not entail the possibility of a verbal report. Primary consciousness refers to the basic condition of being aware of something. This ability is shared by humans and animals with limited semantic capabilities and no true language (Edelman & Tononi, 2000). Humans are also capable of (presumably) higher-order forms of consciousness, which can involve linguistic abilities. In particular, reflective consciousness allows subjects to perceive and describe their own actions and

[2] These notions are not far from Fodor's ideas concerning the neural bases of *normal* cognitive modularity: "…hardwired connections indicate privileged paths of informational access... If you facilitate the flow of information from A to B by hardwiring a connection between them, then you provide B with a kind of access to A that it doesn't have to locations C, D, E.... Neural architecture... is the natural concomitant of information encapsulation" (Fodor, 1983, p. 98f.).

thoughts. To illustrate this distinction, Merleau-Ponty (1942) gave the example of someone who enters a room and feels an impression of disorder, only to later discover that this impression came from a crooked picture on the wall. Before discovering that, this person's consciousness was "living things that it could not spell out." This would by no means imply that the first impression on entering the room was *unconscious*. Rather, the crooked picture generated a form of consciousness whose source was not immediately amenable to verbal description. Only when consciousness assumes a more reflective form is accurate verbal description possible.

3.1. Dissociations in consciousness: the case of endogenous orienting

Consistent with these notions, people can use endogenous strategies of attentional orienting without being able to subsequently describe them. This seems counterintuitive, because the possibility of verbal report is usually considered as inherent to purposeful activities, and endogenous orienting is generally considered to be voluntary or strategic (Jonides, 1981; Posner & Snyder, 1975). In a recent series of experiments (Bartolomeo et al., 2007a; Decaix *et al.*, 2002), normal participants were requested to perform a Posner paradigm with peripheral cues. Cues could either be non-predictive about the target location, when the target appeared at the cued box or at the uncued one with 50% probability, or they could predict the location of the impending target, when targets occurred in the cued box either 80% or 20% of the time. Unknown to participants, cues changed their informative value from non-predictive to predictive during the course of the experiment. Participants' response times changed accordingly, for example by becoming faster for cued targets when cues became 80% predictive. The influence of predictability on response times is usually taken as an example of endogenous, or voluntary orienting (Posner *et al.*, 1982); participants take advantage of the

information conveyed by the cue in order to build an expectation about the locus of target presentation. As a consequence, spatial attention is allocated to the expected position, with faster responses when the target appears at that location. In our experiments, we observed precisely this pattern of results, although participants had received no instructions concerning the information given by the cues. Interestingly, only about half of participants were subsequently able to correctly describe the cue-target relationships ("verbalizers"), thus demonstrating reflective consciousness of endogenous orienting. However, also the remaining participants, those unable to describe the information conveyed by cues, showed a similar RT pattern, thus indicating the occurrence of endogenous orienting without reflective consciousness. Thus, in our experimental setting endogenous orienting could occur independent of verbal reportability. Presumably, all the participants had primary consciousness of cues and targets, and developed accurate knowledge about their relationships, but not all of them could develop the reflective consciousness necessary to verbally describe this knowledge. Thus, this evidence appears to support the phenomenological distinction between primary and reflective consciousness.

3.2. In search of the neural correlates of distinct forms of consciousness

Does the primary/reflective distinction suggested by these behavioral results map onto distinct neural correlates? In a follow-up study using a similar behavioral paradigm (Bartolomeo *et al.*, 2008), participants were scanned with fMRI during performance of the task. The previous behavioral results were replicated. Again, all participants were able to take advantage of the information associated with cues, but only half were subsequently able to describe the cue-target relationships. fMRI showed that both "verbalizer" and "non-verbalizer" participants demonstrated FP activity typically observed in spatial attention tasks (see, e.g., Fig. 2). In addition, verbalizers demonstrated stronger activity in a few

additional structures, including the anterior cingulate cortex (ACC). The finding of increased ACC activity in verbalizer participants is broadly consistent with the proposed role of medial frontal cortex in purposeful behavior and in the monitoring of its consequences (Ridderinkhof *et al.*, 2004). The ACC, with its wide-ranging cortical and subcortical connectivity, seems ideally suited to integrate the activity of different neural assemblies, situated in brain regions far from one another. As discussed above, this integration is likely to be a necessary condition for consciousness to emerge (Dehaene *et al.*, 2006; Edelman & Tononi, 2000). Reflective consciousness, necessary to accurate verbal report, might require an even broader long-distance integration than primary consciousness. If so, a comparatively higher activity of ACC might be expected in reflective consciousness.

In order to be able to verbally report a perceptual experience, I must be able to relate this experience to my perceiving it. Thus, intuitively, reflective consciousness appears to require a certain degree of self-awareness. Many fMRI studies dealing with self-awareness and self-representation have found activations in regions of the medial prefrontal cortex, including the ACC, as opposed to more lateral FP activity in perceptual awareness of external stimuli (see, e.g., Goldberg *et al.*, 2006). Thus, an important role of self-related cortical systems could be "to allow the individual to report about the occurrence of his sensory experience to the outside world" (Goldberg et al., 2006, p. 337). Taken together, these results suggest that primary and reflective forms of consciousness might have partially distinct neural correlates.

3.3. Varieties of consciousness: Implications for the attention/consciousness debate

The distinctions between exogenous/endogenous attention and between primary and reflective forms of consciousness may help clarifying the terms of the debate about the relationships between attention

and consciousness. For example, Wyart and Tallon-Baudry (2008) recently reported the finding of different neural signatures (as indicated by relative activity at different frequencies in the MEG signal) for the process of visual awareness and spatial attention. Participants had to perform a perceptual discrimination on near-threshold stimuli, which were spatially precued by central symbolic cues, 65% of which were valid. Thus, these central informative cues manipulated endogenous attention. On the other hand, awareness was probed by introspective report after stimulus presentation, and thus required reflective consciousness. Attended stimuli were identified more often than unattended ones, but consciously seen stimuli induced increased mid-frequency gamma-band activity over the contralateral visual cortex, whether attended or not, whereas spatial attention modulated high-frequency gamma-band activity in response to both consciously seen and unseen stimuli. These results support the hypothesis of distinct neural architectures mediating endogenous spatial orienting and reflective consciousness. However, they do not negate the possibility, outlined here, that exogenous attention, which can operate independently from endogenous orienting (Berger *et al.*, 2005; Berlucchi *et al.*, 2000; Chica *et al.*, 2006; Lupiáñez *et al.*, 2004), has a closer relationship to visual awareness.

The distinction between primary and reflective forms of consciousness may also help dealing with a further point made by Koch and Tsuchiya (2007), who proposed that attention can be independent of consciousness not only in psychophysical experiments, but also in everyday life. According to Koch and Tsuchiya, much of our everyday behavior is unconscious, in the sense of being automatic. E.g., after driving home from work we could find ourselves unable to verbally report all of our perceptions, which suggests that when driving we used "zombie behavior". However, the distinction between primary and reflective forms of consciousness helps qualifying this example. The inability to verbally report the events I encountered when driving home does not mean that I was

unconscious of these events when they happened, but only that they were unremarkable enough to prevent a more reflective processing (including, perhaps, memory encoding). In other words, "automatic" processing may well entail an inability to report what has been processed, but this is not a sufficient reason to identify automatic processing with the absence of consciousness (Tzelgov, 1997).

4. Conclusion and perspectives

The study of the relationships between two poorly understood and theoretically problematic concepts, such as attention and consciousness, may help constraining hypotheses about their functioning and neural correlates. Activity in many cortical areas, including V1, and extrastriate visual cortex, seems to be necessary but not sufficient for visual consciousness to emerge (Rees *et al.*, 2002). It is possible that additional activity in FP networks is needed to achieve conscious processing, perhaps through the ignition of a global neural broadcasting (Dehaene et al., 2006). Interestingly, these large FP networks seem to be at least in part co-extensive with the brain networks active during the operations of spatial attention (Bartolomeo, 2006; Corbetta & Shulman, 2002; Nobre, 2001; Rosen et al., 1999) and of memory (Naghavi & Nyberg, 2005).

Evidence from neuroimagery (Dehaene et al., 2006) and from neurophysiology (Del Cul *et al.*, 2007) suggests a relationship between FP activity and primary consciousness. Also the dramatic deficit of primary consciousness demonstrated by patients with visual neglect, as a consequence of the disruption of large-scale FP networks, seems broadly consistent with this hypothesis. It remains to be established why right-hemisphere lesions are much more likely to impair awareness of contralateral objects than damage to the left hemisphere. As suggested above, one possibility is that the right hemisphere contains attentional networks particularly important for exogenous orienting.

The proposed distinction between primary and reflective consciousness may open new perspectives in the search for the neural correlates of consciousness.

As reviewed above, there are several FP systems, connected by distinct white matter pathways. Appropriate reflective consciousness of a perceptual event may need the coordinated activity of more than one of these systems. For example, inter-hemispheric coordination among large-scale systems may be necessary for appropriate verbal reports (a behavioral correlate of reflective consciousness), as suggested by the possibility of left-hemisphere based confabulations in split-brain patients and in patients with neglect.

The FP activity which correlates with primary consciousness might not be sufficient for reflective consciousness to emerge. If so, verbal reportability might depend on the activity of large-scale systems partly distinct from the lateral FP networks implicated in spatial attention and important for primary consciousness. For example, at least when introspection is at issue (i.e. subjects have to describe their own states, feelings or strategies), more medial brain systems might be implicated (Bartolomeo et al., 2008; Goldberg et al., 2006).

Despite the theoretical and empirical difficulties in the search of the neural correlates of attention and consciousness, the evidence reviewed here strongly suggests that an important condition for both to occur is the necessity for an integrated functioning of large-scale brain networks. The qualitative distinction between attention and inattentive processing, as well as that between conscious and unconscious processing, might ultimately depend not on the type of information processed, or on the identity of specific cortical areas, but on the amount of integration between distinct processes or large-scale brain systems. It is also apparent that exploring these complex and exciting issues demands

a trans-disciplinary integration of several sources of evidence, such as phenomenology, with its sophisticated treatment of introspective reports, behavioral evidence from experimental psychology, and neuroscience of normal and brain-damaged persons. Thus, there seems to be an intriguing analogy between the demands for integration of remote sources of information in attentive/conscious processing on the one hand, and in research on attention/consciousness on the other hand.

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Figure legends

Fig. 1. Time course of the costs and benefits associated with exogenous and endogenous orienting of attention toward a cued location (modified from Müller & Findlay, 1988). SOA, Stimulus-Onset Asynchrony.

Fig. 2. Hemispheric specialization of attentional functions according to Corbetta and Shulman (2002). FEF, Frontal Eye Fields; IPL, Inferior Parietal Lobule; IPs, Intra-Parietal sulcus; SPL, Superior Parietal Lobule; TPJ, Temporal-Parietal Junction; IFG, Inferior Frontal Gyrus; MFG, Middle Frontal Gyrus. Modified from Doricchi et al (in press).

Fig. 3.A: Schematic rendition of branches II and III of the superior longitudinal fasciculus (SLF) in the monkey (redrawn from Schmahmann & Pandya, 2006); B: Their putative human homologues (yellow, SLF II; green, SLF III), as demonstrated by diffusion tensor imaging tractography (from Thiebaut de Schotten et al., in press).

Fig. 4. Copy of a linear drawing by a patient with right hemisphere damage and left neglect.

Fig. 1

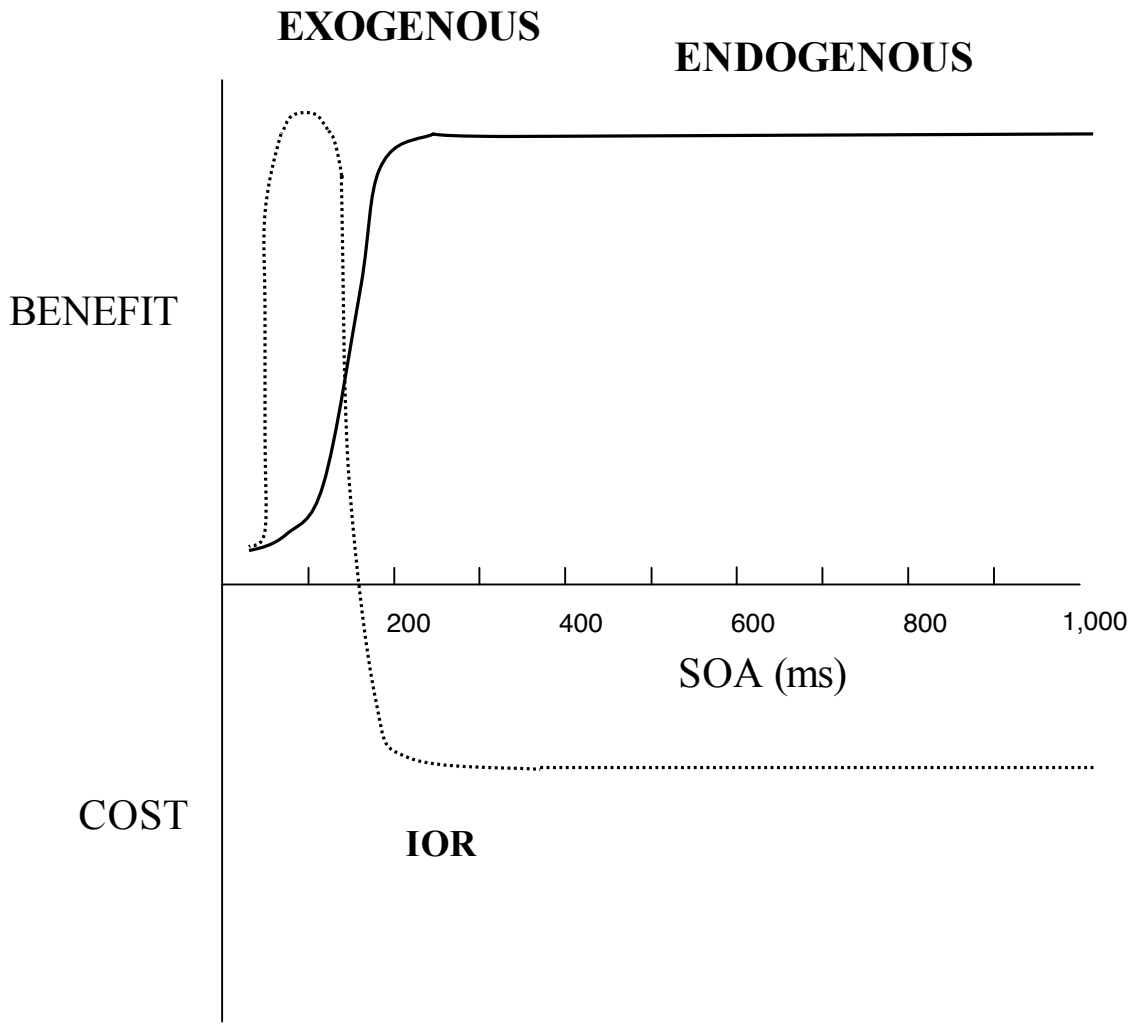
EXOGENOUS
ENDOGENOUS
BENEFIT
200
400
600
800
1,000
SOA (ms)
COST
IOR

Fig. 2

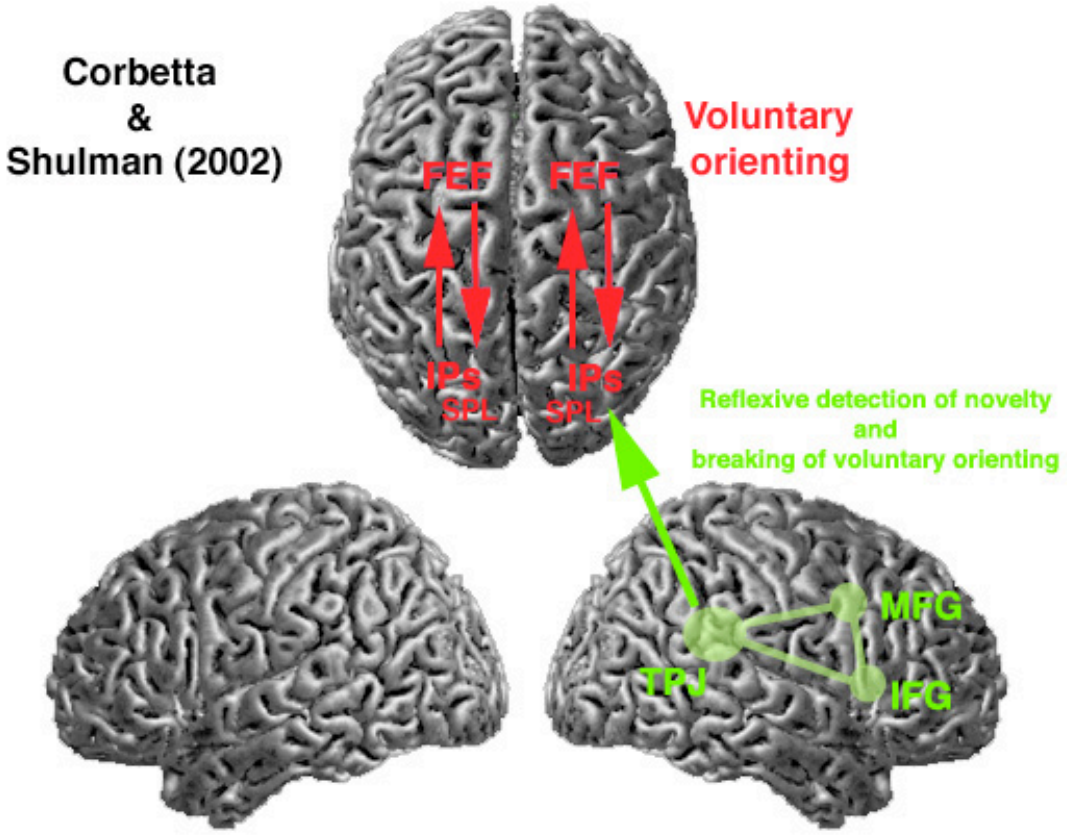
Corbetta
&
Shulman (2002)
Voluntary
orienting
FEF
FEF
IPs
SPL
IPs
SPL
Reflexive detection of novelty
and
breaking of voluntary orienting
MFG
TPJ
IFG

Fig. 3

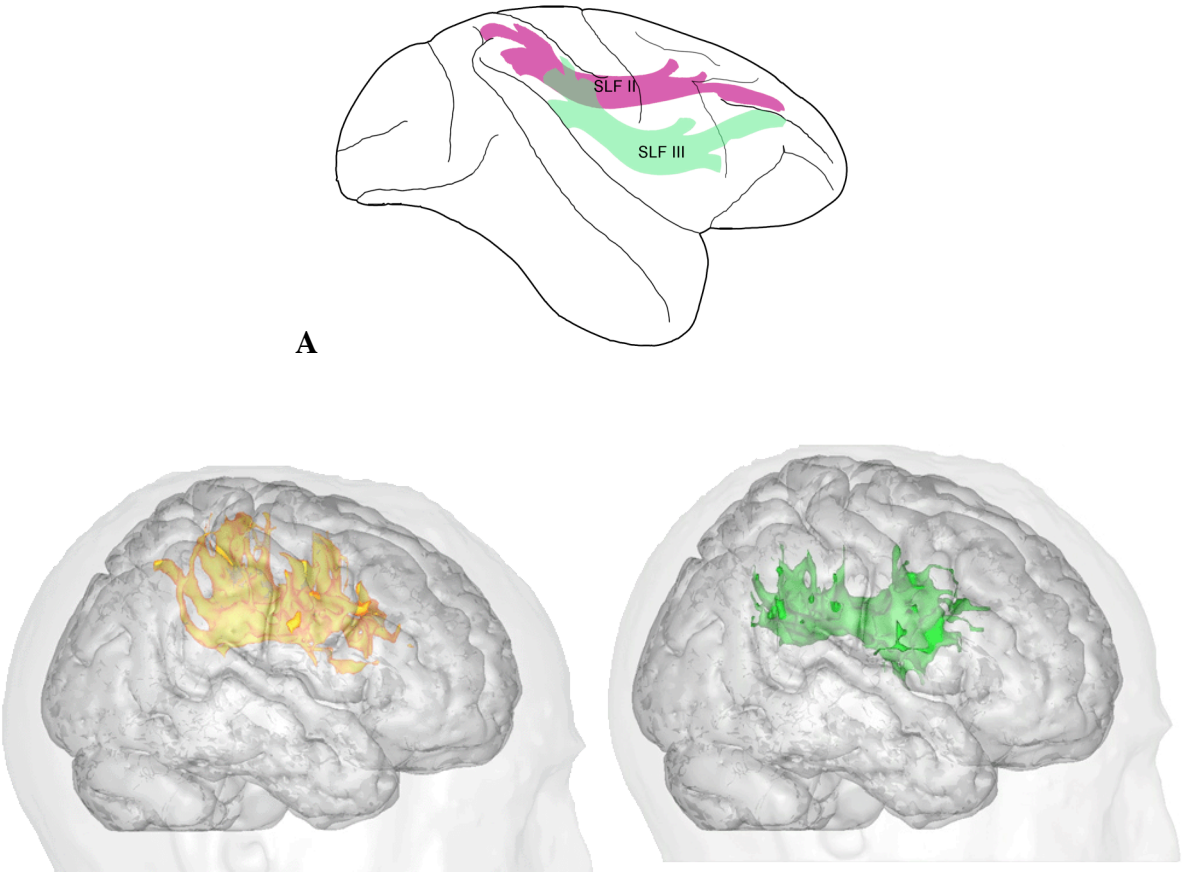

Fig. 4